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ON THE TAXONOMIC STATUS OF FRITILLARIA PHAEANTHERA EASTW. (LILIACEAE)

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The identity and geographical distribution of *Fritillaria phaeantha* Eastw. and *Fritillaria phaeantha* Purdy have been the subject of some confusion. Several issues involved have been discussed by Furse (1969). It is pointed out here that these two homonyms apply to different taxa, and the question of priority is resolved by renaming the later homonym *F. phaeantha* Eastw., to which I give the name *F. eastwoodiae*. The probable origin of *F. eastwoodiae* as a hybrid between *F. recurva* Benth. and *F. micrantha* Heller is explored. Pollination experiments were carried out to confirm the interfertility of the latter two species, and seeds of the cross *F. recurva* (♀) × *F. micrantha* (♂) have been germinated.

The confusion began when Purdy (1932) published a photograph labelled *F. phaeanthera*, together with a brief diagnostic description, following one of *F. lanceolata*. No type was cited, so the type of *F. phaeanthera* Purdy is here designated as the photograph and original description. Both photograph and description ("*F. phaeanthera*, a slender related species, in which the anthers are red, and the petals rather twisted") are those of *F. lanceolata* Pursh var. *gracilis* Wats. (Watson, 1879) from Napa Co., California. As Furse has noted, the publication of Purdy's description precedes that of Eastwood (1933).

A study of Purdy's correspondence to Eastwood, in the archives of the California Academy of Sciences, reveals the reason for this confusing situation. On 22 March, 1932, Purdy sent a specimen of *Fritillaria* from east of Middletown (Lake Co., California) to Eastwood for identification. A few weeks later, the type material of *F. phaeanthera* Eastw. was collected by Mrs. J. H. Morrison near Durham (Butte Co.), and Eastwood recognized the Durham plant as a new species. She apparently wrote to Purdy, incorrectly identifying his plant as *F. phaeanthera*, an as yet unpublished name. Although Eastwood's letter making the identification cannot be found, its content can be inferred from Purdy's reply of 7 May, 1932, acknowledging her identification and noting that he had a good photograph of his plant which he intended to publish in an article in the R.H.S. Lily Year Book (Purdy, 1932). A possible reason for Eastwood's misidentification is that one of the diagnostic characters used by her (indeed the source of the epithet '*phaeanthera*') is the dark red color of the anthers, a character which is also found in *F. lanceolata* var. *gracilis*.

The taxonomic confusion was continued by Beetle (1944) and Munz (1959) who cite locations for *F. phaeanthera* Eastw. in Butte Co. (the type locality of *F. phaeanthera* Eastw.) and in Napa Co. (a locality of *F. lanceolata* var. *gracilis* Wats.). In the text of Beetle's monograph she gives a further location as Plumas Co. but does not cite a specific specimen. However, a specimen from Quincy, Plumas Co. (*Luke Gill s.n.*, DS) was annotated by Beetle as *F. phaeanthera* Eastw. but is *F. atropurpurea* Nutt. with linear, ascending, scattered leaves and open campanulate flowers.

Eastwood's plant (*F. phaeanthera* Eastw.) is a distinct species belonging to a rather difficult taxonomic unit, intermediate between *F. recurva* Benth. and *F. micrantha* Heller. It has been suggested by Beetle (1944) that it arose as a hybrid between *F. recurva* and *F. micrantha*. Although there is little experimental or definitive cytological evidence to establish this as yet, the circumstantial evidence in favor of the hypothesis is compelling and will be reviewed below. Since the epithet *phaeanthera* was previously used by Purdy, I propose a new name for Eastwood's plant, and include an expanded description.

Fritillaria eastwoodiae Macfarlane = *Fritillaria phaeanthera* Eastwood, Leaf. West. Bot. 1:55, 1933, not *F. phaeanthera* Purdy, Roy. Hort. Soc. Lily Year Book 1:97, 1932.

Perennial herb. Bulb 1.5–2.5 cm diam., a sub-conical, enlarged stem base, surrounded by several fleshy scales and numerous rice-grain bulb-lets. Stem 20–80 cm tall, simple, terete, glaucous, flecked with purple near the base. Leaves on upper $\frac{2}{3}$ of stem, in 1–2 whorls of 3–5 below, scattered above, blades linear to narrowly lanceolate, 4–9 mm wide, 5–10 cm long, often glaucous. Flowers (2)3–5(7), racemose, nodding, campanulate, ca 15 mm long and as broad, pale greenish-yellow, apricot, to red. Perianth segments six, narrowly elliptic, 3–5 mm wide, 10–17 mm long, flaring to partially recurving at the tips, sepals narrower and more acute than petals. Nectary lanceolate, less than $\frac{1}{3}$ the length of tepals. Androecium: filaments contiguous near their base, attenuate to the tips, stamens equalling or exceeding pistil before anther dehiscence, but not after; anthers cultrate, ca 5 mm long before dehiscence, red; pollen rust to yellow in color. Gynoecium: style divided in three less than $\frac{1}{2}$ its length, style branches recurving somewhat; pistil often absent in upper flowers. Capsule 6-angled, winged, truncate, ca 15 mm tall and as wide. Chromosome numbers: $n = 18$, near Cherokee, Butte Co. RM 202536 (Beetle 1944); $n = 12$, $12 + f$, near Magalia, Butte Co. JEPS 55690, $n = 17$, $18 + f$, $16 + 2f$, Pinkston Canyon, Butte Co. (Cave 1970); $2n = 24 + 2f$, near Magalia, Butte Co. (Marchant, pers. comm.).

TYPE: Near Durham, Butte Co., California, 17 Apr 1932, Mrs. J. H. Morrison (Holotype CAS 194148!; isotypes: CAS!, K!, GH!).

DISTRIBUTION AND HABITAT: California, Butte Co. and S Shasta Co. Dry slopes, chaparral, foothill woodland, in sun to partial shade, in stony soil with leafmold, on serpentine formations, 400m–1000m. Flowering April–May.

SPECIMENS EXAMINED: CALIFORNIA: De Sabla May 1917, Helen M. Edwards (NY); Feather R. near Yankee Hill, Butte Co., 23 Apr 1922, A. A. Heller 13618 (DS, WTU); occasional about shrubbery in leafmold in the Yellow Pine forest . . . above the reservoir beyond Magalia, 1 May 1938, A. A. Heller 15058 (DS, MO, WTU); on a serpentine outcrop about 4 mi from Magalia on the Coutolenc Rd., Butte Co., 8 Apr 1939, A. A. Heller 15367 (DS, MO, NY, PH, UC, WTU); near Cherokee (pres. Butte Co.), a few in clusters, serpentine soil, 1 Mar 1942, V. Holt (RM); in ponderosa pine woods S of Shingletown, Shasta Co., 21 Apr 1959, R. Bacigalupi 7019 (JEPS); Pinkston Canyon, Big Bend Rd to Yankee Hill, Butte Co., 1800 ft, with *Arctostaphylos viscida*, *Berberis dictyota*, *Dichelostemma volubile*, *Brodiaea californica*, 18 Jun 1960, G. E. See and H. M. Beard s.n. (JEPS); near Magalia, Butte Co., 15 Apr 1967, Margaret Williams s.n. (RENO); near Magalia, Butte Co., E slope amongst bunch grass in the open at the S end of cypresses (a few scattered Douglas Fir and pines), growing in sand and humus amongst serpentine gravel, 16 Apr 1967, W. Roderick s.n. (JEPS); N side of Butte Ck. near Honey Run covered bridge, Butte Co., in wet area, soil a sandy clay, associates *Meconella californica*, *Brodiaea laxa*, 26 Mar 1971, T. C. DeWitt 8 (HSC).

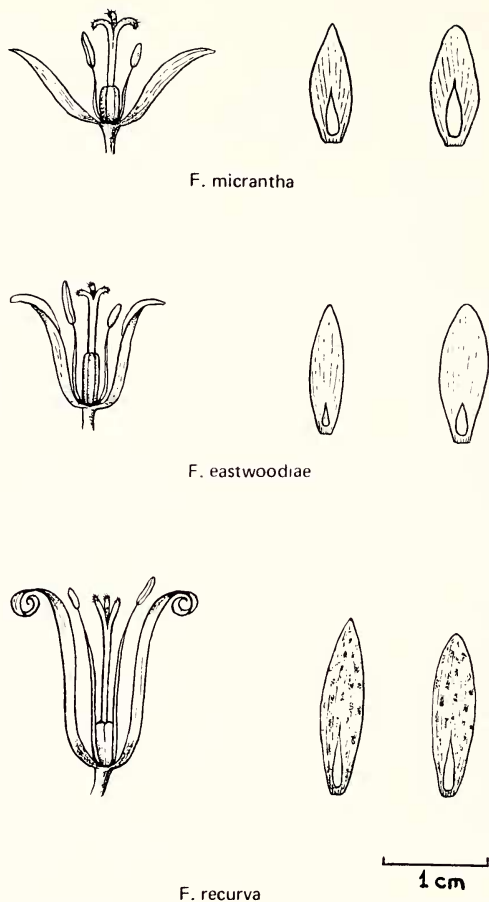


FIG. 1. Floral characters of *Fritillaria micrantha*, *F. eastwoodiae* and *F. recurva* showing (left to right) a) longitudinal section of flower with dehisced and undehisced anthers; b) sepals with nectary in outline; c) petals with nectary in outline.

It will be seen from the above that the first collection of *F. eastwoodiae* was in 1917 at De Sabla, about 20 mi NE of the type locality (it was then identified as *F. coccinea*). In view of the confusion between Eastwood and Purdy, it is interesting to note that the next collection of *F. eastwoodiae*, by Heller in 1922, was identified by him as *F. lanceolata* var. *gracilis* Wats.

The name *Fritillaria eastwoodiae* commemorates Alice Eastwood, long time curator of the California Academy of Sciences herbarium, and author of *Fritillaria brandegei*, *F. eximia*, *F. purdyi*, and *F. striata*.

Without flowers there are few reliable morphological characters separating the species *F. recurva*, *F. micrantha*, *F. eastwoodiae* and *F. lanceo-*

lata var. *gracilis*. A diagnostic key is given below based on floral characters, some of which are illustrated in Fig. 1.

Nectary less than $\frac{1}{3}$ the length of tepals, flowers campanulate to narrowly campanulate, style divided less than $\frac{1}{2}$ its length, style branches not strongly recurving.

Tepals 20–25 mm long, red with yellow tessellation, recurving at their tips 1. *F. recurva*

Tepals 10–15 mm long, red, orange, or pale green, rarely showing tessellation, straight to flaring at their tips 2. *F. eastwoodiae*

Nectary greater than $\frac{1}{3}$ the length of tepals, flowers open-campanulate, style divided more than $\frac{1}{2}$ its length, style branches strongly recurving.

Flowers inconspicuously tessellated, sepals narrower than petals 3. *F. micrantha*

Flowers conspicuously tessellated, sepals broader or approximately equal to petals 4. *F. lanceolata* var. *gracilis*

The tepal color in both *F. micrantha* and *F. lanceolata* var. *gracilis* is purple-brown or rarely greenish, but the nectary of *F. lanceolata* var. *gracilis* is longer and generally more conspicuous.

We return now to the question of the hybrid origin of *F. eastwoodiae*. Its geographical distribution lies at the intersection of those of *F. recurva* and *F. micrantha* (see the distribution map in Fig. 2). It should be stressed that in this region it occurs as a series of stable populations, not as sporadic individuals of recent hybrid origin. Pollination experiments in the field show that the plants are self-sterile but produce normal capsules when unprotected from visits by pollinators. This is the case in all other N. American species studied, viz. *F. atropurpurea*, *F. lanceolata*, *F. micrantha*, *F. pluriflora*, and *F. recurva*. It was also noted by Rix (1976) in E. Mediterranean species, and it is believed that in general *Fritillaria* are obligate outcrossers. The regular production of seed capsules in populations of *F. eastwoodiae* containing diploids therefore suggests that these are normal outbreeding populations.

Typical *F. eastwoodiae* is found on serpentine and it is therefore plausible that the mode of speciation involved stabilization of the hybrid, via apomixis, in a habitat not occupied by either of the alleged parents. Not all regions of overlap provide such a habitat, e.g., near Nevada City, Nevada Co., *F. recurva* and *F. micrantha* are found, but not *F. eastwoodiae*.

There are several other characteristics which strongly suggest hybrid origin. First, the floral characters, which are the main points of distinction in this group of species, place *F. eastwoodiae* intermediate between *F. recurva* and *F. micrantha*—e.g., the flower and tepal shape and color, and the style division (see Fig. 1). *Fritillaria eastwoodiae* shows a rather

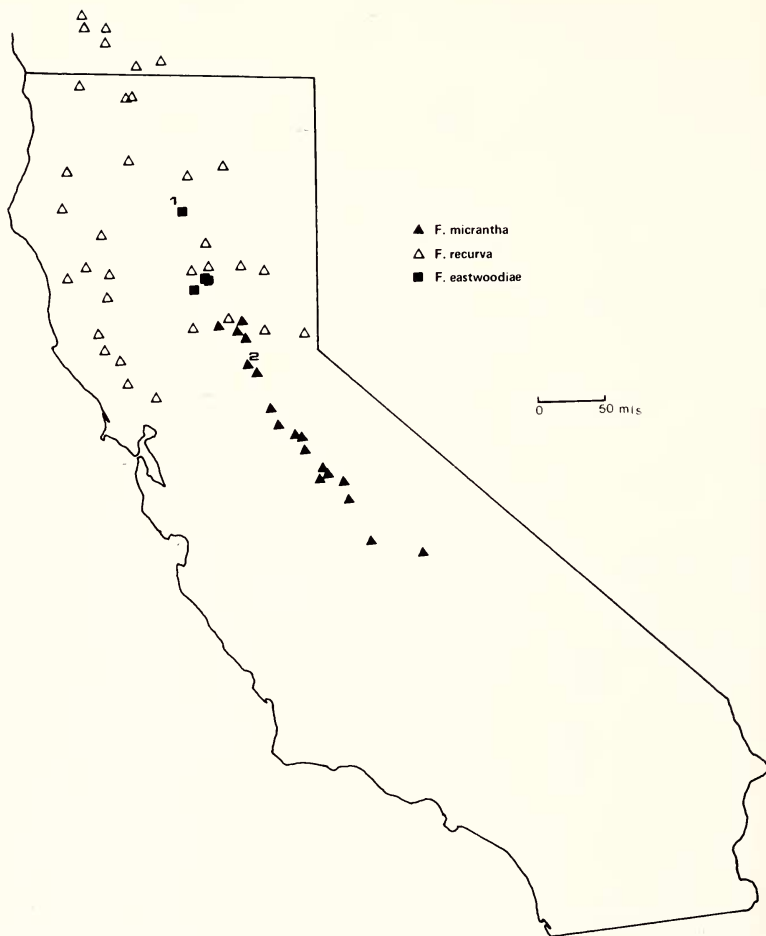


FIG. 2. Distribution map showing the occurrence of *F. eastwoodiae* in California, at the intersection of the distributions of *F. micrantha* and *F. recurva*. 1 denotes a location with possible backcrosses between *F. eastwoodiae* and *F. recurva*; and 2, between *F. eastwoodiae* and *F. micrantha*.

large variation in flower color and shape even in one population, but the flowers are smaller than in *F. recurva* and do not have strongly recurving tepals or prominent yellow tessellation. Second, *F. eastwoodiae* shows irregularities in chromosome pairing at meiosis (Cave, 1970) and frequent cases of female sterility (ovary and style absent). Many individuals which have been studied cytologically are triploids. Somatic cell counts give $2n = 36$ and pollen grains in a given individual show variable chromosome numbers distributed around $n = 18$ (Cave, 1970). This behavior is expected as a result of meiosis in the triploids. As noted

earlier, diploid plants also occur and seed capsules are regularly produced. Finally, controlled pollination of *F. recurva* (♀) by *F. micrantha* (♂), and also the reverse cross, yielded capsules about 80% of the seeds of which had normally developed embryos. Seeds from a single capsule of *F. recurva* (♀) × *F. micrantha* (♂) showed better than 50% germination, suggesting that interspecific sterility barriers do not exist between these species. In particular, the endosperm of the hybrid seed does not appear to contain embryo growth inhibitors such as have been found in *Lilium* (Emsweller *et al*, 1962) and suspected in the case of E. Mediterranean *Fritillaria* (Rix, 1971).

The diversity of flower form found in *F. eastwoodiae* is probably due in part to the frequent occurrence of triploids with their associated sexual sterility, and to a stabilization of the diversity by vegetative propagation which exists via the rice-grain bulblets produced in great abundance. The mechanism for producing triploids is not clear. No tetraploid individuals of *F. recurva* or *F. micrantha* which potentially could be parents in a triploid-diploid hybrid are known. Indeed, tetraploidy is rare in N. American *Fritillaria*, only one case having been reported (in *F. lanceolata* by Beetle, 1944). This is true of the genus as a whole, and is probably due to the large size of the chromosomes, which might inhibit cell division in the tetraploid condition (Darlington, 1932; Grant, 1971). If it were not for this, allotetraploidy would provide a convenient route to bypass hybrid sterility. A more likely hypothesis is that triploids have been formed many times from unreduced gametes, and these individuals, because of their well-developed habit of vegetative apomixis, have survived as clones. The triploid character apparently confers some constitutional advantage, since the triploids have competed successfully with diploid parents and siblings, which have both sexual and vegetative channels available to them. The possibility of agamospermy is being investigated. Chromosome counts have been done on only a few individuals of the *F. eastwoodiae* complex (Cave, 1970), but it is interesting that the only diploids reported (from Magalia, Butte Co., Cave, 1970; Marchant, pers. comm.) are also the most intermediate morphologically and geographically between *F. micrantha* and *F. recurva*. Individuals closer to *F. recurva* (e.g., *R. Bacigalupi* 7019, JEPS 25404 from Shasta Co.) are triploid, and possibly represent backcrosses to *F. recurva*. Similarly, triploid plants have been found in El Dorado Co. (*W. Roderick s.n.*, JEPS 55692) which are close morphologically and geographically to *F. micrantha* and perhaps represent backcrosses to the latter (see Fig. 2). Whether unreduced gametes function more effectively in the backcrosses remains, however, a matter of speculation, since populations of typical *F. eastwoodiae* contain both diploid and triploid individuals. The origin of *F. eastwoodiae* needs further investigation, e.g., by a study of the degree of heterozygosity using chromosome banding patterns (La Cour, 1951; Dyer, 1963).

Finally, the probable hybrid origin of *F. eastwoodiae* raises an interesting question regarding pollinators, since one of the supposed parents, *F. recurva*, is hummingbird pollinated (Grant and Grant, 1968; D. Santana, pers. comm.) whereas the other, *F. micrantha*, with its open brownish-green flowers and much less abundant nectar, almost certainly is not. This suggests that hummingbirds are not the exclusive pollinators of *F. recurva*.

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